

10.0 ESTIMATING SURVIVAL

10.1 Introduction

There is a considerable variety of ways to estimate survival. Many of the available methods come as by-products of methods designed primarily for measuring population size (Chapter 8), and are thus best discussed in reference to that problem. However, knowledge of survival is sufficiently important to justify specific studies without special reference to determining population size. Such efforts are usually dependent on some form of marking or tagging. Since marking is almost always a very expensive and time-consuming operation, it should, wherever possible, also result in estimates of population numbers. However, we will here be concerned mainly with measuring survival.

A survival rate is necessarily defined for some unit of time, thus:

$$\begin{aligned}\text{Survival rate} &= \frac{\text{Number alive at end of period}}{\text{Number alive at start of period}} \\ &= \text{proportion surviving the period.}\end{aligned}$$

When dealing with populations exploited by hunting or fishing it is frequently necessary to consider two components of mortality, one due to the exploitation and the second to all other causes of death ("natural" mortality). When the two different forces of mortality exist at the same time, only one can actually result in a given death, so it is customary to speak of "competing" sources of mortality or "competing risks."

If a population is "closed", that is, has no gains or losses from immigration, births, or emigration, the simplest model for mortality or survival is just the binomial distribution. If N represents initial population size, and p the proportion dying during some interval, then the expected number of deaths is simply Np , and the probability of various numbers of deaths is given by terms of the binomial distribution. Similarly if fractions can be assigned to exploitation and to natural mortality, then the model becomes a multinomial distribution.

In practice it is necessary to be cautious in using a simple model. Mortality seldom operates as a simple random variable as required by the model. In exploitation in particular, there is usually a tendency for events resulting in deaths to come in "bunches", violating the postulate of independence. Furthermore, mortality almost always varies seasonally, and exploitation usually is restricted to particular seasons. Also, when animals are tagged in groups, they are likely to stay clustered to some extent.

Another point is that we rarely know the total population size or the total numbers of deaths, and must estimate survival or mortality through some sampling process. In spite of all of this, the binomial model frequently provides a useful starting place (but usually not with total population as a parameter). Certain special populations do fulfill many of the requirements for the binomial and multinomial models. These are normally experimental populations being subjected to, e.g., chemicals to determine lethal effects of various dosages ("bioassay").

The principal methods for estimating survival or mortality may be categorized as follows:

I. From tagging or marking

A. Multiple recoveries of marked individuals

1. Capture-recapture methods. As mentioned above, estimates of survival or mortality are usually auxiliary to population estimation. These methods usually involve a series of captures and releases of individuals.

2. Multiple recoveries of individuals all tagged at the same time. Not a commonly used technique.

B. Single recovery of a marked individual. Normally the tag recovery comes coincident with death of the individual.

1. Recovery effort variable. For the most part, this pertains to exploitation, and the effort expended in hunting or fishing is that considered as devoted to recovery.

2. Constant recovery effort. Very often this is a necessary, but untested assumption. It may be reasonably acceptable where tag recovery depends on accidental death of individuals.

a. Exact time of death known. This is an area not much explored in biological studies, but well known industrially under the heading of "life-testing", where the survival of interest is that of some manufactured product (e.g., light-bulbs).

b. Time of death not known exactly. This is the category into which the bulk of methods in current use fall.

II. Other methods

A. Catch-effort methods. In commercial fisheries studies, much attention has been paid to assessing population size through measuring the rate of change in catch with accumulated effort. It may also be possible to estimate mortality at the same time.

B. Change-in-ratio methods. Also known as "dichotomy" or "survey-removal" methods, these depend on knowing the magnitude of a removal and observing a ratio before and after the removal. Survival may be concurrently estimated.

C. Catch-curves or kill curves. The age structure of animals taken in harvests may provide some notion of the year-to-year survival rate. It is usually necessary to assume constant population size and constant annual survival.

It is perhaps worthwhile to mention life tables here. In the original application, a life table served to record survival information down through the history of a particular group of individuals or to reflect the current state of survival rates in a population. In ecological studies there has been a

common tendency to arrange the returns from tagging in a life table, and this has led to some rather dubious calculations.

10.2 A single-recovery model

If a group of tagged individuals are released together and have a constant survival rate thereafter, then a fairly simple model suffices and permits various useful estimates. What happens when the assumption of constant survival does not hold is not known in any detail, but some rough guidance is available. It should be noted that the frequent practice of estimating annual survival from tag recoveries may not be importantly influenced by seasonal changes in survival, so long as the annual rate remains relatively constant. The other major use of single-recovery data is for relatively short-term periods (usually in seasons of exploitation) wherein it may reasonably be assumed that survival is approximately constant.

The most thorough analysis to date of the relevant model is one by Chapman and Robson (1960) which actually pertained to catch-curves, but also applies directly to tag recoveries, as pointed out by Paulik (1962). We will follow that analysis here. Let:

N_0 = initial population (number tagged or number alive at the time analysis starts -- this last assumption may be used to avoid effects of a higher early mortality).

s = constant survival rate (per unit of time)

λ = fraction of number currently alive that are caught and reported (in a given time unit). This may be the product of two constants, one being "catchability" and the second, reporting rate. Note that λ is used elsewhere here as a rate of population change, but is used in this case to correspond to the paper of Chapman and Robson (1960).

n_x = number of tagged individuals recovered in x th time unit. Confusion in notation can arise here, depending on how time units are numbered. One naturally speaks of the "first" time unit, but it is useful to let $x = 0, 1, 2, \dots$, and to suppose that n_0 represents those individuals who fail to survive through the first time unit. Under the above assumptions and definitions, it turns out that the probability of recovering a given individual in the x^{th} time unit follows a geometric probability distribution:

$$p_x = (1-s)s^x \quad x = 0, 1, 2, \dots \quad (10.1)$$

and the expected numbers of recoveries are:

$$E(n_x) = N_0 \lambda s^x \quad x = 0, 1, 2, \dots \quad (10.2)$$

This seems intuitively obvious, since if λ represents "catchability" the entire population is available in the first year, but only survivors are "at risk" in subsequent years.

The actual recoveries in any particular time unit constitute a binomial random variable, with probability given by (10.1) above, so that:

$$\Pr\{n_X \text{ individuals recovered}\} = \binom{N_0}{n_X} (\lambda s^X)^{n_X} (1-\lambda s^X)^{N_0-n_X} \quad (10.3)$$

If one wants to consider the distribution of recoveries over a set of time periods, then it is possible to consider the conditional distribution as being approximately a multinomial distribution. That is, for a fixed total sample $n = n_0 + n_1 + \dots + n_k$, the joint probability distribution

$$\Pr\{n_0, n_1, n_2, \dots, n_k \mid n\}$$

is a multinomial with the P_i corresponding to equation (10.1) above.

Chapman and Robson (1960) have shown that the best estimate for s is:

$$\hat{s} = \frac{T}{n+T-1} \quad (10.4)$$

where:

$$\begin{aligned} n &= n_0 + n_1 + n_2 + \dots + n_k \\ T &= n_1 + 2n_2 + 3n_3 + \dots + kn_k \end{aligned}$$

That is, n is just the total recoveries, and $n + T$ is effectively the "total years survived" after tagging. An estimate of the variance is:

$$v(\hat{s}) = \hat{s} \left(\hat{s} - \frac{T-1}{n+T-2} \right) \quad (10.5)$$

It is important to note that the method assumes that essentially all tagged individuals are dead when the analysis starts--a modified formula for partially complete recoveries will be described later.

The Chapman-Robson estimator is nearly identical to one generally attributed to D. Lack, but first studied mathematically by Haldane (1955). It is:

$$s = \frac{T}{n+T} \quad (10.6)$$

so the two estimators will differ only for small samples. The variance obtained by Haldane is (method of maximum likelihood):

$$v(s) = \frac{s(1-s)^2}{n} \quad (10.7)$$

a little algebra permits comparison of the two variance estimates:

$$\frac{\text{Chapman-Robson variance}}{\text{Lack-Haldane variance}} = \frac{n(n+T-1)}{(n-1)(n+T-2)} \quad (10.8)$$

which shows that the Lack-Haldane estimate will be a little smaller than the "best" estimate, but not importantly so if the number of recoveries is at all sizable.

A simple way to obtain the Lack-Haldane estimator is to use equation (10.2) and obtain expected values for n and T as follows:

$$E(n) = E(n_0) + E(n_1) + \dots = N_0\lambda(1 + s + s^2 + \dots)$$

and summing the infinite geometric series, we have:

$$E(n) = \frac{N_0\lambda}{1-s} \quad E(T) = E(\sum x n_x) = N_0\lambda(0 + s + 2s^2 + \dots) = \frac{N_0\lambda s}{(1-s)^2}$$

If the "mean age at death" is defined as:

$$\bar{x} = \frac{T}{n}$$

then substituting expected values for T and n :

$$\frac{E(T)}{E(n)} = \frac{s}{1-s} \quad \text{and} \quad \hat{s} = \frac{T}{n+T} \quad (10.9)$$

Example 10.1 Chapman-Robson survival estimate

As an example of the use of equations (10.4) and (10.5) we consider some data on band recoveries from adult Canada geese (Rutherford, 1970:27) banded as adults in the Arkansas Valley of Colorado in the 1950-51 season. A total of 344 geese were banded, with recoveries in subsequent years as follows:

<u>Year of recovery following banding</u>	<u>Number of recoveries</u>
x	n_x
0	45
1	23
2	19
3	10
4	7
5	12
6	5
7	3
8	3
9	2
10	2
11	0
12	1
13	1
14	0
15	1
Total recoveries (n)	134

$$T = 23 + 2(19) + 3(10) + 4(7) + 5(12) + \dots + 15(1) = 332$$

$$\hat{s} = \frac{T}{n+T-1} = \frac{332}{134+332-1} = 0.714$$

$$v(\hat{s}) = \hat{s} \left(\hat{s} - \frac{T-1}{n+T-2} \right) = \frac{332}{465} \left(\frac{332}{465} - \frac{331}{464} \right) = 0.0004401$$

so that the standard error of the estimated variance is $(.0004401)^{1/2} = 0.021$ and approximate 95 percent confidence limits on the survival estimate are given by $.714 \pm 2(0.021)$ or 0.672 to 0.756.

10.3 Further estimators

One very simple procedure is to consider the fraction n_0/n , which represents the fraction dying in the first time interval and thus estimates a mortality rate. Conversely, survival can be estimated as:

$$s_0' = 1 - \frac{n_0}{n} = \frac{n-n_0}{n} = \frac{n_1 + n_2 + \dots + n_k}{n_0 + n_1 + n_2 + n_k} \quad (10.10)$$

where n_k represents the oldest group from which any recoveries are obtained (we again assume all tagged individuals are dead before calculations begin, so no new recoveries can be expected). The above estimate is attributed to Heincke (1913) and a minor modification (dropping n_k from the denominator of the right-hand expression) yields an estimator proposed by C. H. N. Jackson (1939).

The Heincke estimate can readily be treated statistically, inasmuch as, for a given total number of recoveries (n), the probability that a particular individual is recovered in the first year is just $p = 1-s$ so the distribution of the number of first year recoveries (n_0) is binomial:

$$\Pr\{n_0 \text{ recoveries in 1st year}\} = \binom{n}{n_0} (1-s)^{n_0} s^{n-n_0} \quad (10.11)$$

so that the expected number is:

$$E(n_0) = n(1-s)$$

which gives the estimate of equation (10.10). The usual binomial estimate of a variance of a proportion then gives a variance as:

$$v(s_0') = \frac{s(1-s)}{n} \quad (10.12)$$

The importance of this result arises by comparison with equation (10.7). The ratio of the two variances is:

$$\frac{v(s_0')}{v(\hat{s})} = \frac{1}{1-s} \quad (10.13)$$

which amounts to a rather remarkable state of affairs, if one stops to consider the substantial costs involved in tag and recovery studies. Supposing annual survival to be on the order of 50 per cent, equation (10.13) shows that the

variance obtained from the Heincke method will be about double that obtained from the preferred methods (Chapman-Robson or Lack-Haldane). This then says that choice of the wrong equation amounts effectively to throwing away half of one's hard earned information, and the older literature abounds with examples where the Heincke estimate is used when the better estimate is available.

10.4 Analysis of incomplete data

In many applications it is necessary to estimate survival from only part of the data. Perhaps the most frequent case is when the investigator cannot afford to wait until nearly all recoveries are back, but must proceed with results from the early recovery periods. Calculations depend on an equation analogous to (10.9) which is:

$$\frac{T}{n} = \frac{s}{1-s} - \frac{(k+1)s^{k+1}}{1-s^{k+1}} \quad (10.14)$$

in which k represents the last recoveries available, and

$$n = n_0 + n_1 + n_2 + \dots + n_k$$

$$T = n_1 + 2n_2 + \dots + kn_k$$

If only two years of recoveries are available $k=1$, and

$$\frac{T}{n} = \frac{n_1}{n_0 + n_1} = \frac{s}{1-s} - \frac{2s^2}{1-s^2} = \frac{s}{1+s}$$

and this gives an estimate of s as

$$\hat{s} = \frac{n_1}{n_0} \quad (10.15)$$

which is what one might intuitively expect--that recoveries in two successive years differ only by s (or this can be obtained by use of equation (10.2)).

If $k=2$ a somewhat more complicated equation can be obtained for estimating s directly (Robson and Chapman, 1961:188), but for larger values of k one must resort to trial and error (iterative) methods or to tables (Robson and Chapman, 1961). Hand calculations are not too awkward, and a starting value can quickly be obtained from equation (10.15).

An estimate of the variance of the estimate is obtained from:

$$v(s^*) = \frac{\frac{1}{n}}{\frac{1}{s(1-s)^2} - \frac{(k+1)^2 s^{k-1}}{(1-s^{k+1})^2}} \quad (10.16)$$

An examination of equation (10.16) shows that as k becomes large, the term involving k tends to become very small, so that the equation reduces to equation (10.7), as it should. With these results, the investigator can determine approximately what the effect will be of estimating survival from only part of the recoveries, as opposed to waiting until all tagged individuals are quite

surely dead. If s is not quite small, there may be a substantial difference in the variability between the two situations. An estimate of the reduction in variability resulting from using all of the recoveries can be obtained by dividing equation (10.7) by (10.16):

$$\frac{\hat{v}(s)}{\hat{v}(s^*)} \doteq 1 - \frac{(k+1)^2 s^k (1-s)^2}{(1-s^{k+1})^2} \quad (10.17)$$

Some selected values are as follows:

	k						
s	1	2	3	4	6	8	10
0.10	0.669	0.927	0.987	0.998	1.0	1.0	1.0
0.20	0.444	0.766	0.918	0.974	0.998	1.0	1.0
0.30	0.290	0.581	0.785	0.900	0.982	0.997	1.0
0.50	0.111	0.265	0.431	0.584	0.806	0.921	0.970
0.70	0.031	0.081	0.145	0.219	0.384	0.544	0.680
0.90	0.003	0.007	0.014	0.022	0.043	0.071	0.104

Inspection of the above table shows the advantage of basing survival estimates on as many periods of recovery as possible.

Example 10.2 Analysis of incomplete data

For an example of "segment" calculations (Eq. 10.14), we again use Rutherford's data, and suppose that only the first 4 classes are available for estimation. Then:

$$n = 45+23+19+10=97$$

$$T = 23+2(19)+3(10)=91$$

$$\bar{x} = \frac{T}{n} = \frac{91}{97} = 0.9381$$

and we enter the tables given by Robson and Chapman (1961) and Seber (1982:584). In the column corresponding to $k = 3$ (4 classes) and find 0.938 to correspond to $s = 0.62$. A convenient alternative is to use SOLVER in EXCEL. A variance estimate (Eq. 10.16) is:

$$\hat{v}(s) = \frac{\frac{1}{97}}{\frac{1}{0.62(0.38)^2} - \frac{16(0.62)^2}{(1-(0.62)^4)^2}} = 0.003816$$

which is much larger than the variance for the complete set of data (0.00044).

10.5 Testing assumptions

The assumption of constant survival and recovery rates is one likely to be violated in many actual situations. We will look briefly at some of the effects of changing rates in a later section. Here we consider ways of looking

for bias. Probably the most useful technique is to have a thorough knowledge of the circumstances in which the data were obtained, and to examine the prospects for any major change that might influence either survival or recovery rates. Another considerable help is to have a rather long series of comparable data to examine for any persistent trends. Most bird-banding experience, for example, shows that juveniles have a markedly lower survival than do adults. Hence one either tries to band mostly adults or deals with juveniles separately.

Some statistical tests may also be considered. One is just the ordinary chi-square goodness-of-fit test, wherein the expected values are computed from $n_x = \hat{n}s^x$ and compared with the observations (n_0, n_1, n_2, \dots) . Substantial departures from constant survival may show up in this test, but it isn't very sensitive, and failure to obtain a significant chi-square needs to be regarded as a necessary condition for use of the estimate but should not be regarded as any substantial evidence against bias.

Fortunately there is a test for one of the major sources of error, i.e., a difference in survival rate between the first recovery - class and subsequent classes. It thus serves very well to examine the effects of, for example, tagging young animals. The test is due to Chapman and Robson (1960) and is a chi-square with one degree of freedom:

$$\chi^2 = \frac{(\hat{s} - s'_0)^2}{\frac{T(T-1)(n-1)}{n(n+T-1)^2(n+T-2)}} \quad (10.18)$$

where \hat{s} is obtained from the Chapman-Robson estimate of equation (10.4) and s'_0 is the Heinke estimate of equation (10.10).

Example 10.3 Testing compatibility of first recoveries

The chi-square test for compatibility of the first recovery-class with the remaining classes (Eq. 10.18) is readily illustrated on the data of Example 10.1. It requires Heinke's estimate of survival (Eq. 10.10):

$$s'_0 = \frac{n - n_0}{n} = \frac{134 - 45}{134} = 0.6642$$

The chi-square test then is:

$$\chi^2 = \frac{(0.714 - 0.6642)^2}{\frac{332(331)133}{134(465)^2 464}} = \frac{0.00248}{0.00109} = 2.28$$

which is well short of the 95 percent significance level of chi-square.

The above test is "two-tailed", that is, operates so as to protect one against either over- or under-representation of the first age-class. If the investigator has good grounds for expecting a departure to be in only one direction (e.g., if mesh size of nets is known to be the critical factor, or greater vulnerability of young game animals), then a one-tailed test may be in order. This can be obtained just by

considering the ratio of $\hat{s} - s'_0$ to the square root of the denominator of Eq. (10.18), and referring to tables of the normal distribution for significance levels (the critical level for a one-tailed test at the 95 percent level of significance is 1.65 rather than the 1.96 used for two-tailed tests). If there were grounds to support doing a one-tailed test here, one could calculate:

$$z = \frac{0.714 - 0.6642}{(0.00109)^{1/2}} = \frac{0.0498}{0.033} = 1.5$$

which is again short of the 95 percent level (1.65).

The above are "large-sample" tests. Chapman and Robson (1960:364) point out that the appropriate "exact" distribution is the hypergeometric, but also that for all practical purposes one may substitute a table of binomial confidence limits, using the statistic $T=(n_1+n_2+n_3+\dots)$ as "sample size" and $T-n+n_0$ as "number of successes". If the selected confidence interval (corresponding to chosen level of significance) excludes s then one rejects the hypothesis of compatibility of survival of the first age group with that of the remaining recoveries. If the above tests suggest incompatibility of the first recovery class, one simply drops that class and recodes his data, so that n_0 is now the first recovery-class retained, n_1 the second, and so on. Calculations of survival and variance, etc., proceed just as before, but its a wise precaution to repeat the above testing procedure to make sure that the new initial recovery group is compatible with the remainder.

Example 10.4 Combining years

In Example 10.1, a large number of geese were banded in one year, resulting in a substantial number of returns and quite a precise estimate of the annual survival rate. Often one must deal with much smaller samples, and the question of combining a series of estimates may then come up. When all, or, virtually all, of the recoveries are in, the procedure is very simple -- just add up the recoveries, and proceed as before (Chapman and Robson 1960:357). Some data on adult Canada geese banded in Washington (Hanson and Eberhardt, 1971) provide an example:

		<u>Recoveries during subsequent years</u>												
Year	Number												Recov.	
<u>banded</u>	<u>banded</u>	n_0	n_1	n_2	n_3	n_4	n_5	n_6	n_7	n_8	n_9	Tot.	Rate	
1950	43	1	2	1			1				1	6	.14	
1951	40	2	2	2			1					7	.18	
1952	133	14	8	7	6	1		2	1	1		40	.30	
1953	13				1							1	.08	
1954	25	3	2	2	1							8	.32	
1955	30	3	2				1					6	.20	
1956	49	1	2	3	1			1		1		9	.18	
1957	38		2	1	2		2	1				8	.21	
1958	45	5	2			2	2		2			13	.29	
1959	34		1	1	1	1				1	1	6	.18	
1960	18	2						1				3	.17	
-----		468	31	23	17	12	4	7	5	3	3	1	107	.23

$$T = 23 + 2(17) + 3(12) + 4(4) + 5(7) + 6(5) + 7(3) + 8(3) + 9(1) = 228$$

$$\hat{s} = \frac{T}{n + T - 1} = \frac{228}{334} = 0.683$$

$$v(\hat{s}) = \frac{228}{334} \left[\frac{228}{334} - \frac{227}{333} \right] = 0.0006506$$

We thus obtain an estimate of annual survival of $.684 \pm 2(0.0006506)^{1/2}$ or confidence limits of 0.634 - 0.735 on the combined estimate.

When several years are combined, as above, it seems prudent to examine the band recovery rates to see whether there is any evidence to suggest a change that might invalidate the underlying assumptions (e.g., a change in reporting rates). One simple procedure is just to do a chi-square test against the overall recovery rate. The calculations here are:

<u>Year</u>	<u>Number banded</u>	<u>Number recovered(q_i)</u>	<u>Recovery rate (p_i)</u>
1950	43	6	0.1395
1951	40	7	0.1750
1952	133	40	0.3008
1953	13	1	0.0769
1954	25	8	0.3200
1955	30	6	0.2000
1956	49	9	0.1837
1957	38	8	0.2105
1958	45	13	0.2889
1959	34	6	0.1765
1960	18	3	0.1667
<hr/>			
	468	107 (A)	0.2035 = \bar{p}

and a handy formula for chi-square is (Cochran and Snedecor, 1967:240):

$$\chi^2 = \frac{\sum p_i a_i - \bar{p}A}{\bar{p}\bar{q}} = \frac{26.5809 - 21.7738}{0.1621} = 29.66$$

with 10 degrees of freedom, indicating strong evidence of a departure from chance fluctuations in proportion recovered.

10.6 Life tables

The original and major use of a life table is to provide a convenient summary of survivorship data over the history of a given group of animals, all born at nearly the same time (a "cohort" and hence a cohort table) or to provide a cross-section of current mortality experience in a population (a "current" life table). As such, there should be no objection to life tables. Unhappily many such tables have been constructed from band-recovery and

age structure data in ways that may greatly reduce the value of the data. Most of this section will be devoted to life tables as constructed from band recovery data.

The basic structure of the table is quite simple, although a variety of modifications and extensions has to be derived for various special purposes. The structure of a "cohort" table is obtained as follows. Most life tables start out with an arbitrary number of newly born animals (usually 1000, or 10,000), and have 4 main columns. The first (x) column lists age at the beginning of the time interval (normally a year), the second (l_x) gives the number alive at the beginning of the year, while the third (d_x) gives the number of deaths during the year, and the fourth column (q_x) represents the mortality rate. Entries in a particular table might thus be:

x	l_x	d_x	q_x
0	1000	620	0.620
1	380	167	0.439
2	213	85	0.399
3	128	51	0.398
4	77	32	0.416
5	45	19	0.422
6	26	14	0.538
7	12	6	0.500
8	6	4	0.667
9	2	2	1.000

Since the table begins with an arbitrary number of animals, the only really important data are those contained in the q_x column, which summarizes the available information on mortality by age. Some cohort tables do start out with the actual number of individuals in a real group, and thus provide more information than does the "standard" table. "Current" life tables are usually constructed in exactly the same way, but depend on different sources of data (i.e., on current mortality experience of a population).

Construction of a cohort life table (also known as a "time specific" life table) from the recovery of marked animals at their death rests on the intuitively plausible concept that the recoveries constitute a representative sample of the fate of the entire group initially marked. The method in common use is to sum up the total recoveries (n) over the years, and to regard this total as a cohort, or "number initially at risk". Thus n may be the first entry in the l_x column -- unfortunately many workers convert it to 1,000 or 10,000, making it impossible (without additional information) to reconstruct the actual data from their table. Those individuals recovered in the first year are then regarded as mortalities (appearing in the d_x column) and the first year mortality rate is estimated as n_1/n . In the second year it is assumed that there are $n - n_0$ survivors (l_1 entry) and the recorded deaths in that year (n_1) appear in the d_1 position and become the numerator in the mortality (q_1) estimate:

$$q_1 = \frac{n_1}{n - n_0}$$

continuing the process yields mortality rates for each year up to the last recoveries (n_k) whereupon the last year's mortality rate becomes $n_k/n_k = 1$.

It thus turns out that the first entry in the table corresponds to the Heincke estimate of equation (10.10), and each successive entry corresponds to the same estimate, with previous recovery-class disregarded. Thus the estimates are not what they have been claimed to be, that is, age-specific mortality rates. They are instead estimates of a constant rate for the whole set of recovery data, and the supposed life table is not at all what it is normally expected to be. Furthermore, as we have seen from equation (10.13) using the Heincke estimate amounts to discarding a sizable fraction of the available data. Some workers did "combine" the several estimates by weighting each q_x estimate by the apparent sample size (n_x), giving:

$$\frac{\frac{n_0}{n} n + \frac{n_1}{n-n_0} (n-n_0) + \dots}{n_0 + 2n_1 + 3n_2 + \dots} = \frac{n}{n + T} \quad (10.19)$$

which is the Lack-Haldane estimate, and thus may well be the only really useful estimate in the whole table. If the actual numbers recovered are entered in the table (rather than converting to 1000 or 10,000 for the l_0 entry) then it is feasible to go back and use the chi-square test of equation (10.18) on the data. Sometimes the total number of recoveries is given separately, so that it is possible to reconstruct the original data from the table, even though l_0 is 1000 or 10,000. At worst, one can look down the q_x column to see whether the apparent mortality rates do change -- but this is seldom a very helpful practice in view of the substantial variability of the Heincke estimates.

Perhaps the best summary statement about cohort tables based on recovery data is that they should not be constructed in the first place. If the basic assumption is fulfilled (constant survival) then each entry estimates exactly the same quantity! If survival rates are not constant over the years, then the structure of the various estimates can be illustrated by writing out the value for the first one:

$$q_0 = \frac{n_0}{n - n_0} = \frac{pN(1-s_1)}{pN(1-s_2)s_1 + pN(1-s_3)s_1s_2 + \dots + pN(1-s_{k+1})s_1s_2\dots s_k} \quad (10.20)$$

where p = recovery rate, N = population tagged, and the s_i are annual survival rates. Thus only if the s_i are all equal to s , do we get conditions for a valid estimate.

When one uses data based on a group of animals all marked at the same time, the applicable life table concept is indeed that of a cohort. However, the data are nonetheless at times used to construct a current life-table (also called a "dynamic" table, and perhaps more accurately so in the present context).

The usual practice seems to be to regard the ratios of successive recovery-classes as estimators of current survival rates, so that:

$$q_x = \frac{n_x}{n_x - 1}$$

and using the notion of equation (10.20):

$$q_x = 1 - \frac{pN(1-s_x)s_1s_2\dots s_{x-1}}{pN(1-s_{x-1})s_1s_2\dots s_{x-2}} = 1 - \frac{(1-s_x)s_{x-1}}{1-s_{x-1}} \quad (10.21)$$

so that, if survival is constant in two successive years, the method does provide a valid estimate. The existence of changing survival rates evidently will result in a bias. Perhaps a more serious drawback is that the samples usually obtained are so small as to result in substantial variability in the year to year estimates. In the majority of cases, it is likely that only the first two or three recovery groups are large enough to justify much confidence in the mortality estimates.

One technique used to reduce the effect of small samples is to combine the recoveries from a number of years of marking, producing what is commonly called a "composite" life table. Sometimes this is done with partially incomplete data. That is, there may be one (or more) sets where all of the recoveries are available, plus several sets where banding was done recently enough so that there is likely to be a number of marked individuals yet alive. In such circumstances an adjustment may be introduced to compensate for the incomplete nature of the data. The adjustment takes the form of computing for each year a "number of marked individuals available." The trick is simply to add up the total number actually banded during the period of interest. This total is regarded as the number "available", and the first year recoveries are divided by that number to generate a " d_0 " class. If the most recent year of banding did not contribute to the second year recoveries then the number banded in that year is subtracted from the total banded, and the remainder is used as a divisor to generate " d_1 " from the second year recovery. The process continues until the number banded in the first year is used as divisor for the last recovery class. Some better methods for calculating survival rates from incomplete data are available, and will be described below.

In summary, many of the methods for generating life tables from banding data are of very dubious utility. The "cohort" method does not do what it is supposed to do at all, and the "current" method suffers seriously from small samples. There is, of course, no reason to object to the construction of life tables from data obtained by recovery of banded animals. The point is that survival estimates should be obtained by the best methods available and then used to construct a life table. The methods already described are quite simple and should normally be less trouble to use than the supposed life table method.

10.7 Catch-curves and kill-curves

It was mentioned above that the Chapman-Robson analysis was originally developed for catch curves but applies equally well for banding data. It thus follows that there is little need to recapitulate the methods of estimation already described. It is necessary, though, to note some pitfalls for the unwary and changes in assumptions. In band-recovery studies, one usually has a known population (the total number banded) under study, and obtains recoveries over a number of time intervals. The essential assumptions are that survival remains constant (or nearly so) and that recovery rates of dead animals also remain constant. On the other hand catch-curves or kill-curves usually depend on an age-classification of a group of animals taken nearly simultaneously (by fishing or hunting) and thus born over a number of years. Constant survival is again a necessary assumption, while the

assumption of constant recovery rates is now replaced by one of equal "catchability" (vulnerability to the harvest method) for each age group. Unfortunately a third assumption has also to be added in that it is also required that each age-group initially exist in equal numbers.

In fisheries studies there is often a problem with the second assumption - - younger fish may be less readily taken by the fishing methods (e.g., mesh size of nets). This problem is usually dealt with by restricting the analysis to start with the first age group considered to be "fully vulnerable to the gear" (which can be checked out with the chi-square test of equation (10.18)). Most fish have a tremendously large reproductive potential so that it seems that the link between size of mature stock and numbers of new recruits may at least be tenable for several years in a row. This is not to deny, of course, the importance of spawner-recruit relationships. The major point is that catch-curves seem to be rather more useful in fisheries work than do kill-curves in studies of hunted populations, and it seems likely that the chief difficulty may lie in the third assumption. Most game populations do not appear to have a sufficiently constant recruitment to permit use of survival estimates from kill-curves for more than very rough estimates.

10.8 Combining estimates from several years

In many cases the available recovery data will come from a number of years of banding. There then may arise the need to combine several sets of data to produce a single survival estimate. As always, one should not blindly combine data from different years but should first examine the individual estimates (along with the standard errors), and review the prospects of any major change between the years in question. All too often recoveries from a single year's banding constitute a very small sample, and they may have to be combined with other years.

The simplest situation arises when there are complete sets of recoveries for a number of years. One then simply adds together the corresponding year-classes (i.e., numbers of recoveries 1,2,3,... years after banding) and uses equation (10.6) to estimate survival, and (10.7) to estimate variance of the estimate.

When the data are incomplete, as discussed in Section 10.4, the calculations become somewhat more tedious. The usual set of data may be represented by the following table:

Maximum age at recovery	<u>"Age" at recovery</u>				<u>Totals</u>
	1	2	3	x	
k	n_k
3	d_{13}	d_{23}	d_{33}		n_3
2	d_{12}	d_{22}			n_2
1	d_{11}				n_1
<hr/>					
Totals	d_1	d_2	d_3	d_x	$\Sigma n_k = \Sigma d_x$

Here the rows are sets of recoveries from a given year of banding, with the most recent year at the bottom -- hence the maximum "age" at recovery is one year. The row totals (n_k) are thus the total number recovered from a given year of banding, while the column totals reflect the total numbers that had been "at large" for a given number (x) of years. "Age" is necessarily reckoned from banding, so that animals banded as adults may in fact be appreciable older than implied by the terminology here.

Actual survival estimates from the above table are obtained from the following equations (Gilmartin et al. 1993):

$$\sum_{j=0}^k \frac{T_j}{n_j} = \sum_{j=0}^k \frac{1}{1-s} - \frac{(k_j+1)s^{k_j+1}}{(1-s^{k_j+1})} \quad (10.22)$$

$$Var(s) = \left[\sum_{j=0}^k \left\{ \frac{n_j}{s(1-s)^2} - \frac{(k_j+1)^2 s^{k_j-1} n}{(1-s^{k_j+1})^2} \right\} \right]^{-1} \quad (10.23)$$

where T_k is computed for each row in just the same way that T was obtained for equation (10.6), i.e.;

$$T_3 = d_{13} + 2d_{23} + 3d_{33}$$

The solution of equation (10.22) depends on iterative methods just as it did for equation (10.14), to which it is closely related -- in fact (10.22) may be obtained by summing equation (10.14) over the total number of years of recovery (i.e., sum on k). Similarly, equation (10.23), stems from summing the equation (10.16).

The method described above was obtained by Haldane (1955) and is fairly well-known as "Haldane method." It may be repeated that a prudent investigator will use equations (10.14) and (10.16) to investigate at least part of the individual years before settling on a combined estimate. If no banding was done in one or more years it is still feasible to use equations (10.22) and (10.23); one just enters zeroes for the years of no banding. Gilmartin et al.(1993) used monte carlo methods to study the variance equation and found that it gave confidence limits that were too wide, so resorted to bootstrapping to estimate confidence limits.

Example 10.5 An example of Haldane's method

For an example of combining incomplete data, we use some band returns data on Canada geese banded in Washington (Hanson and Eberhardt, 1971) as adults:

Year banded	No. banded	Maximum age at recovery	"Age at recovery"							Tot.
			0	1	2	3	4	5	6	
1961	14	6	3	0	2	1	0	0	0	6
1962	15	5	0	2	0	0	1	0		3
1963	28	4	4	4	1	1	0			10
1964	45	3	3	2	2	6				13
1965	10	2	0	1	0					1
1966	0	1	0	0						0
1967	15	0	2							2
<hr/>										
			12	9	5	8	1	0	0	35

We first compute T_k and n_k for each row in just the same manner as T was computed before:

$$\begin{aligned}
 T_6 &= 2(2) + 3(1) &= 7 & n_6 &= 6 \\
 T_5 &= 2 + 4(1) &= 6 & n_5 &= 3 \\
 T_4 &= 4 + 2(1) + 3(1) &= 9 & n_4 &= 10 \\
 T_3 &= 2 + 2(2) + 3(6) &= 24 & n_3 &= 13 \\
 T_2 &= 1 & & n_2 &= 1 \\
 T_1 &= 0 & & n_1 &= 0 \\
 T_0 &= 0 & & n_0 &= 0
 \end{aligned}$$

and s is estimated by solving equation (10.22) by trial and error. One sets up the table above in EXCEL and computes the components of equation (10.22) in two columns, sums these and varies s until the two column sums are equal. If there are several examples to compute, the solution might be obtained with SOLVER.

10.9 Regression methods

Recalling equation (10.2):

$$E(n_X) = N_0 \lambda s^X$$

If we take logarithms:

$$\log E(n_X) = \log(N_0 \lambda) + x \log s \quad (10.24)$$

and ordinary linear regression methods might be used to fit observed data and to estimate s as the slope of the regression of $\log n_X$ on years since banding. Such a procedure has the additional merit that one can examine the plotted data for any evidence of non-linearity, and hence for prospects of a change in survival with time.

A disadvantage of the regression method is that band recovery data do not conform to the requirements for regression estimation. Chapman and Robson (1960) suggest an improvement in some cases may be obtained by using

$$\log n_x - \frac{1}{n_x + 1}$$

as the independent variable (rather than just $\log n_x$). They further recommend dropping all observations beyond the point where n_x is less than 5.

It is important to realize that the regression equation estimates $\log s$, and not s . If natural logarithms are used, the quantity

$$i = \log_e s$$

is the "instantaneous" rate of survival, and is rather widely useful in fisheries work as such. A natural temptation is to antilog the estimate of $\log s$ for a direct estimate of s ; unfortunately this yields a biased estimate and there doesn't seem to be much to do about it unless the samples are large. But with quite large samples the bias may not be important.

Paulik (1963) developed another regression-like method based on the fact that recoveries in a number of years approximately follow the multinomial distribution (this was mentioned in Section 10.2). His results seem to offer an improvement over the simple regression estimate (10.24). His estimate is:

$$\log \hat{s} = \frac{\sum j n_j y_j - [(\sum n_j y_j)(\sum n_j) / \sum n_j]}{\sum j^2 n_j - [(\sum j n_j)^2 / \sum n_j]} \quad (10.25)$$

where $j = 1, 2, 3, \dots$ denoted the year of recovery (with the first year's recoveries now numbered as n_1 rather than n_0 as before). Also;

$$y_j = \log_e \left(\frac{n_j}{N} \right)$$

which is the natural logarithm of the proportion (of N banded) in the j^{th} year. Paulik recommended deleting observations beyond the point where $n_j = 10$.

Since this method also estimates the logarithm of s and not s directly, it may be best applied in circumstances where interest is not so much in estimates of annual survival, but is rather directed towards components of that survival rate, expressed in terms of the instantaneous rates. That is, fisheries workers customarily write

$$s = e^{-(F+M)}$$

where F = mortality rate (instantaneous) from fishing and M = mortality rate (instantaneous) from other causes (the "natural" mortality rate), and the regression methods thus estimate the quantity $F+M$ directly. Any auxiliary information on the intensity of exploitation during the time periods when the data were collected may potentially permit an estimate of the relative contribution of F to total mortality.

One other reason for considering estimates of $\log(s)$ rather than s is that $\log(s)$ may be roughly normally distributed. This may be a considerable advantage in making tests of comparisons or in setting confidence limits. If

$\log(s)$ is normally distributed, then the antilog $e^{\log s}$ will be lognormally distributed (and thus have a skewed distribution -- awkward for many purposes.)

10.10 Effect of changes in survival

We recall that one of the key assumptions in the analysis of both band recovery and kill-curve data is that the survival rate remain constant over the period of study. In practice, survival undoubtedly does vary from year to year. If the annual fluctuation are not large and are more or less "chance" events, presumably the estimates may provide some sort of average value. Very often, though changes in survival rate may persist for several years. This is especially true for exploited populations, where shifts in management regulations may induce changes in survival.

Not a great deal is known about the effect of persistent changes on estimation of survival, but some indication of trend can be supplied. We first consider band recoveries, and assume the recoveries come from an exploited population (tags are recovered from the harvested animals). Suppose fishing or hunting (F_X) and natural (M_X) mortality operate together over the year (and remain constant during the year) but change from year to year. If we let

$$f_X = \frac{F_X}{F_X + M_X}$$

then the estimate of survival from recoveries is approximately:

$$\begin{aligned} \frac{E(T)}{E(n+T)} &= \\ \frac{E(n_1) + 2E(n_2) + 3E(n_3) + \dots}{E(n_0) + 2E(n_1) + 3E(n_2) + \dots} & \quad (10.27) \\ &= \frac{f_1(1-s_1)s_0 + 2f_2(1-s_2)s_0s_1 + 3f_3(1-s_3)s_0s_1s_2 + \dots}{f_0(1-s_0) + 2f_1(1-s_1)s_0 + 3f_2(1-s_2)s_0s_1 + 4f_3(1-s_3)s_0s_1s_2 + \dots} \\ &= s_0 \frac{f_1(1-s_1) + 2f_2(1-s_2)s_1 + \dots}{f_0(1-s_0) + 2f_1(1-s_1)s_0 + \dots} \end{aligned}$$

Thus if the samples are large enough to permit the operation of equation (10.27) -- one would really prefer to find $E(T/n+T)$ which is not the same as what we have above -- it appears that the "dominant" quantity in the estimate is s_0 , or survival in the first year. One might expect that result by inspection of the recovery data, since the first two classes (n_0 and n_1) are necessarily expected to be the largest. The effect of some postulated change in survival rates can be determined by considering the sequence of survival rates in equation (10.27). For example, suppose survival has been increasing so that $s_0 > s_1 > s_2$. Then $(1-s_1) > (1-s_0)$ and $(1-s_2) > (1-s_1)$, and so on. Consequently the overall estimate will be less than s_0 . One might thus write:

$$\hat{s} = s_0(\text{bias})$$

Any quantitative appraisal of the bias term will evidently depend on a numerical evaluation of equation (10.27) for which one needs to know survival rates. Furthermore, changes in survival are likely also to affect the f_x terms, inasmuch as the fraction taken by exploitation will no doubt also change.

While the situation above is rather complex from an analytical standpoint, the circumstances are not difficult to mimic via computer simulation. A limited effort along those lines (Eberhardt, 1972) led to the following set of recommendations:

(1) The Chapman-Robson (Lack) equation for estimation of survival from banding recoveries is clearly the best of those studied. The other methods have variances which are usually at least twice as large.

(2) Both Chapman-Robson and Heincke estimates should always be computed and used to test the compatibility of the first year of returns actually used with those of later years. If the test is significant, one may simply drop the first year, and proceed with the remaining data.

(3) In the case of incomplete data (banded individuals still alive at analysis) or a prior evidence of a marked change in survival rates, the segment method is available, but variability of the results is discouragingly large unless the data are nearly complete.

(4) Combining results of a series of years of banding may take two routes.

(a) If it appears that there is a marked change in survival, one probably has to depend on a year-to-year analysis--this is an area needing further investigation.

(b) If it appears that survival rates have not changed appreciably, then those years for which complete data are available can simply be added together and analyzed with the Lack formula (justification for this statement appears in the appendix to Eberhardt (1972)). If part of the data is incomplete, then the Haldane formula is called for.

(5) It was provisionally suggested that, even in the face of changing rates, the Chapman-Robson and/or Heincke methods give estimates of first-year survival which likely are not very much biased. An exception is the case where rates change in the second year, as may be expected if first-year recoveries of juvenile banding are used. However, the Chapman-Robson test provides good protection against that eventuality.

(6) If all else fails, and samples are indeed large, one might look at ratios of successive groups of returns (i.e., use the "current" life table) and obtain an average survival rate. Even so, it is probably advisable to simply drop the smaller frequency groups (say below 10 returns).

(7) There seems to be little reason to continue the practice of life-table analysis of banding data. Under the requisite assumptions, all of the information in a "cohort" table appears in its first line, and in the form of a

Heincke estimate, which has a variance appreciably larger than that of the preferred method. Use of the method thus amounts to throwing away data that are often rather expensive to obtain. As suggested above (6), it may be necessary to examine data on a year-to-year basis--essentially in a "current" life table, but the variances of such estimates are discouragingly large. The evidence from this study suggests that the Chapman-Robson (Lack) method will often give a useful estimate of first-year survival, and that very likely will be all that can effectively be salvaged.

Much the same sort of analysis can be carried out for kill-curves. In analogy to equation (10.2):

$$\begin{aligned}
 E(n_x) &= \lambda N s_1 s_2 \dots s_x \dots \\
 \frac{E(T)}{E(n+T)} &= \frac{\lambda N (s_1 + 2s_1 s_2 + 3s_1 s_2 s_3 + \dots)}{\lambda N (1 + 2s_1 + 3s_1 s_2 + 4s_1 s_2 s_3 + \dots)} \quad (10.28) \\
 &= s_1 \left[\frac{1 + 2s_2 + 3s_2 s_3 + \dots}{1 + 2s_1 + 3s_1 s_2 + \dots} \right]
 \end{aligned}$$

and we can again consider changes like $s_1 > s_2 > s_3$ and their qualitative effect on a bias term:

$$\hat{s} = s_1(\text{bias})$$

It is perhaps worth noting what happens if survival remains constant for several years, e.g.:

$$s_1 = s_2 = s_3 > s_4 = s_5 = s_6$$

if we let s_1 represent the recent series and s_2 the older series of rates, we have

$$\frac{E(T)}{E(n+T)} = s_1 \frac{1 + 2s_1 + 3s_1^2 + 4s_1^3 s_2 + \dots}{1 + 2s_1 + 3s_1^2 + 4s_1^3 + \dots}$$

so that, unless survival is unusually high so that the later terms have an influence, it seems evident that the estimate will be very close to s_1 , apart from the effects of sampling variation.

A similar analysis can be carried out for the Heincke estimate (equation (10.10)):

$$\frac{E(n-n_0)}{E(n)} = s_1 \frac{1 + s_2 + s_2 s_3 + \dots}{1 + s_1 + s_1 s_2 + \dots} \quad (10.29)$$

A crucial assumption in the above is that recruitment remains constant, i.e., that we can consider N to be a constant in developing equations like (10.28). As we have already remarked, this is frequently an unwarranted assumption, and this largely negates direct use of the methods thus far described for kill-curves of many populations.

10.11 Use of telemetry to estimate survival

Radiotelemetry offers substantial advantages over depending on tag returns for estimating survival. Conceptually, the actual time of death will be

known and it may be possible to determine the cause of death for non-harvest mortalities. Under such circumstances a simple binomial model may suffice for analysis. Very likely the most widely known analysis is that of Heisy and Fuller (1985). They proposed estimating a daily survival rate as:

$$s_i = \frac{x_i - y_i}{x_i} = 1 - \frac{y_i}{x_i} \quad (10.30)$$

Where x_i is the total number of transmitter-days, and y_i is the total number of deaths in some interval, i . An important precaution is to select an interval in which conditions are likely to be relatively constant. It may be necessary to consider several such intervals that span the total period of interest. For a single such interval the survival rate may be estimated as:

$$S_i = s_i^{L_i} = \left(1 - \frac{y_i}{x_i}\right)^{L_i} \quad (10.31)$$

Combining rates for several intervals is then accomplished by multiplying the rates for the several (I) intervals

$$S^* = \prod_{i=1}^I S_i \quad (10.32)$$

10.12 Kaplan-Meier estimates of survival

An important problem in survival estimation is lack of knowledge of the fate of individuals. The difficulty is severe when tags or bands are recovered by sampling as in hunting and fishing, but is also important in the capture-recapture methods. Conceptually, it should be a minor concern in radiotelemetry studies where one might suppose there is virtually absolute knowledge of the fate of individuals. However, this is not always the case. Radios do fail on occasion, as do the attachments, and the lost radiotag may not always be promptly recovered. Also, radiotagged individuals may emigrate out of the study area, which may pose a special problem that needs to be considered in the study design.

The problem of the loss of identity of individuals turns up in various other circumstances. It is particularly important in medical studies, where the long-term fate of patients given some treatment needs to be followed for many years. Various forms of "life-testing" also bring up the issue, inasmuch as some items may be removed from the study for reasons that have no bearing on the duration of life of the item. These difficulties led to a study of ways to deal with the incomplete observations by Kaplan and Meier (1958). It has been proposed that their methods for compensating for inadvertent losses be used in radiotelemetry studies. (Pollock et al. 1989).

The basis for the Kaplan-Meier approach is to handle the individuals lost from the study ("censored" observations) by breaking the records down in intervals and estimating survival separately for each such interval. Overall survival for a longer period is estimated from the product of the individual intervals just as in equation (10.32). It turns out that the approach of Heisy and Fuller (1985) described above can be used to give essentially the same results,

but it is worthwhile to contrast the two methods inasmuch as the calculations proceed somewhat differently.

Kaplan and Meier (1958) term their procedure a “product-limit” estimate. It depends on a sequence of events (deaths and losses from observation) that are assumed to be mutually exclusive in terms of the time of occurrence, i.e., occur at different times. They suggest “fudging” a little if two events are recorded at the same time. If data are recorded by day, there may not be much need for “fudging”. Very likely losses from observation may be less-accurately recorded as to date, and Kaplan and Meier (1958:461) recommended that “deaths recorded as of an age t are treated as if they occurred slightly before t , and losses recorded as of an age t are treated as occurring slightly after t ” (this is only necessary if two events are recorded at exactly the same time).

To introduce the basic scheme, we assume no losses and consider only deaths as events, plotted along a line representing the time span (of length L_1) being considered.

+-----*-----*-----*-----+
0 1 2 3 ... d-1 d L

If d deaths occur and the initial population size is N , then probability of the first death is $1-(1/N)$, and given that event, then the probability of the second event is $1-[1/(N-1)]$, and so on, with the probability of d deaths being the product of the individual terms:

$$(1 - \frac{1}{N})(1 - \frac{1}{N-1})(1 - \frac{1}{N-2}) \dots (1 - \frac{1}{N-d+1})$$

Rearranging gives:

$$(\frac{N-1}{N})(\frac{N-2}{N-1})(\frac{N-3}{N-2}) \dots (\frac{N-d}{N-d-1})$$

Cancelling like terms in numerator and denominator reduces the result to:

$$S(L_i) = \frac{N-d}{N} = 1 - \frac{d}{N} \quad (10.33)$$

Which is what one would expect, i.e., survival rate equals $1 - \text{mortality rate}$.

The approach of Heisy and Fuller previously discussed might be labeled the “radio-days” method for convenient reference. It uses a daily survival rate and estimates survival for the same span (L_1) as:

$$S_i = (1 - \frac{d}{X})^{L_i} \quad (10.34)$$

Where X is the sum of the days lived by the animals dying in L_1 plus the $(N-d)$ L_1 days from animals that did not die during the observed time span. Thus the product-limit (Kaplan-Meier) method uses a mortality rate based on population size while the “radio-days” method expands a daily rate to the overall interval used. The time span considered can be varied to accommodate one’s immediate

purpose. Pollock et al. (1989:Table 1) illustrate the method using weekly data. Their Table 1 with Heisy-Fuller calculations added shows the agreement between the two methods:

Week	Number at risk	Deaths	Censored	Kaplan-Meier Survival	Cumulative weeks	Cumulative deaths	Heisey- Fuller Survival
1	18	0	0	1	18	0	1
2	18	0	0	1	36	0	1
3	18	2	0	0.8889	54	2	0.8930
4	16	0	0	0.8889	70	2	0.8905
5	16	0	0	0.8889	86	2	0.8890
6	16	1	0	0.8333	102	3	0.8360
7	15	0	0	0.8333	117	3	0.8337
8	15	1	1	0.7778	132	4	0.7818
9	13	1	2	0.7179	145	5	0.7292
10	10	1	1	0.6462	155	6	0.6738
11	8	0	0	0.6462	163	6	0.6620
12	8	0	1	0.6462	171	6	0.6514
13	7	0	0	0.6462	178	6	0.6403

The data above are cumulated over the span of the study, which, as noted previously, assumes constant survivorship. If there is reason to suppose that survival is not constant, then the data should be analyzed in blocks that are more likely to have constant survival within a block. In many studies, captures may go on throughout the course of the study. Kaplan and Meier (1958) noted that these individuals can be added to the number at risk as they enter the study, and Pollock et al. (1989) dubbed such an approach as a "staggered-entry" model, and illustrated it with weekly data on bobwhite quail (*Colinus virginianus*) survival. They provided a convenient variance estimate [Heisey and Fuller (1985) resorted to a computer program for variance estimation]:

$$v[S(t)] = \frac{S(t)^2[1 - S(t)]}{r(t)} \quad (10.35)$$

where $r(t)$ is the number at risk at time t . Data to illustrate the approach from their Table 2 appear below with variance estimates. In this case sequential survival estimates [equation(10.33)] are multiplied [equation (10.32) to obtain an estimate of survival at the end of the current period. To use the Heisey-Fuller approach on the data, one would have to determine how long the individuals dying during the period (week) were alive during the period, so that it is desirable to record radio-days as best possible. In the table below it is assumed that individuals censored were lost at the end of the period and any added were introduced at the end of the period.

Kaplan-Meier estimates of survival for bobwhite quail [from Pollock et al. (1989: Table 2)] with variance estimates.

Week	Number at risk	Deaths	Censored	Added	Kaplan-Meier Survival	Variance
1	20	0	0	1	1	0
2	21	0	0	1	1	0
3	22	2	1	0	0.909	0.0034
4	19	5	0	0	0.670	0.0078
5	14	3	0	0	0.526	0.0094
6	11	0	0	0	0.526	0.0119
7	11	0	0	0	0.526	0.0119
8	11	2	0	0	0.431	0.0096
9	9	1	0	0	0.383	0.0100
10	8	0	1	0	0.383	0.0113
11	7	0	0	3	0.383	0.0129
12	10	0	0	6	0.383	0.0090
13	16	4	0	10	0.287	0.0037
14	22	4	0	5	0.235	0.0019
15	23	4	1	6	0.194	0.0013
16	24	4	0	0	0.162	0.0009
17	20	2	0	0	0.146	0.0009

10.13 More complex models for analysis of survival data.

Much of this Chapter has been devoted to what might now be termed “classical” methods for estimating survival. The older methods remain valuable as a background for understanding the newer approaches, and they provide tools for initial analyses and for planning studies. The major drawback in using these earlier methods is the restrictive assumptions that are required to justify the estimates. Section 10.10 provides some rough notions about the outcome of using these estimates when the underlying assumptions are violated.

The newer, “modern”, methods make it possible to use less restrictive and more realistic assumptions, and to take advantage of the computing power now available on most desktops. A disadvantage of the newer methods is the nearly universal dependence on computer programs. A major goal of the present effort has been one of presenting the basis for many quantitative methods without requiring the reader to use any more complex programs than are available on most spreadsheets, with specific reference to EXCEL. For the most part, only basic statistical methods have been used. To use the newer methods, one needs to rely on computer programs, along with more sophisticated statistical methods.

A good starting-place for approaching “modeling survival and testing biological hypotheses using marked animals” is the paper by Lebreton et al. (1992). They recommend (1) starting from a “global” model (essentially one that includes all the parameters that may be relevant) and assess its fit, then (2) select a more parsimonious model (fewer parameters) using Akaike’s Information Criterion (AIC), and (3) testing for the more important biological questions by comparing this model with “neighboring ones” using likelihood

ratio tests, and then (4) find maximum likelihood estimates of model parameters with estimates of precision. Papers utilizing this general approach are now steadily appearing in the ecological literature, and it appears likely that the approach has become the “standard” method for studying survival.

Using AIC in biological studies is the subject of a recent book (Burnham and Anderson 1998) that contains a good deal of practical advice on model selection and inference. It appears, however, that these authors have developed doubts about the importance of a “global” model, at least in contrast to an earlier essay (Burnham and Anderson 1992), and they particularly warn of the dangers of “data-dredging”, i.e., starting with a model with many parameters and discarding parameters by using AIC. The problem basically is that chance fluctuations in the data may seriously influence the outcome, essentially in the manner that plagues stepwise regression (Section 1.12). Burnham and Anderson (1998) thus recommend choosing a “parsimonious” model on largely a priori grounds. How one does that is still an open question in many situations. However, the rapidly developing literature on modeling survival offers opportunities to select a few models that seem to be among the top candidates and thus useful starting-places.

Lebreton et al. (1992) list a sizable number of computer programs that have been used to estimate survival and used RELEASE which is described in detail by Burnham et al. (1987) and SURGE 4.0, which was (and still may be) a proprietary program. Fortunately, Dr. G. C. White has invested a great deal of effort in producing and updating program MARK which contains most of the features of these earlier versions and is freely available through the Web Site listed in Section 8.4.

10.14 Exercises

10.14.1 Calculate the Heinke estimator of survival and its variance for the data of Example 10.1. Calculate the ratio of its variance to that of the Haldane variance estimate [eq.(10.7)]. Compare this ratio to the value you get from eq.(10.13). Is there a difference? If so, explain.

10.14.2 Repeat the analysis of Example 10.2, then extend it to use the first 6 classes and calculate a variance estimate from eq.(10.16). Compare this variance estimate with that of example 10.1, and with the value of the ratio tabulated below eq.(10.17). Discuss your results.

10.14.3 Check on the values tabulated for eq.(10.17) for $k = 6$ and explain the trend from $s = 0.1$ to $s = 0.9$.

10.14.4 Suppose that there were 55 recoveries in the first year after banding in Example 10.1 (instead of 45 recoveries). Compute the chi-square test for compatibility of first recoveries and state the p-value.

10.14.5 Calculate the chi-square value for Example 10.4.

10.14.6 The following resighting data are for female monk seals on Laysan Island. Calculate a survival rate as in Example 10.5. Compute a variance from eq.(10.23). As noted in Section 10.8, it likely is best to bootstrap for confidence intervals, but the estimate should serve for comparison to the results of Exercise 10.14.7 below.

	Tagged	0	1	2	3	4	5	6	7
1983	10	10	10	9	8	9	9	6	6
1984	13	12	10	10	8	7	6	6	
1985	14	10	9	9	7	5	5		
1986	17	12	12	9	7	6			
1987	15	13	11	9	7				
1988	17	11	5	4					
1989	13	6	6						

10.14.7 The following data are resightings for female monk seals banded on French Frigate Shoals in 1984. Calculated survival from eq.(10.24) along with a variance about regression (you can do this with EXCEL's regression tool). Compare this variance with that found in Exercise 10.14.6. Also calculate s from eq.(10.25) and compare with the results of eq.(10.24) and Exercise 10.14.6.

Tagged	1	2	3	4	5	6	7
39	35	35	33	30	28	26	26